

external nutrient concentrations at each time step. This allows algal growth to be computed using conventional Michaelis-Menten kinetics, but at the same time allows the internal stoichiometry of the algae to vary. Since the cells are assumed to equilibrate immediately with the external nutrient concentrations during transport, both the computational difficulties associated with the rapid uptake dynamics and the problem of algae with different internal stoichiometries being transported into the same model segment are eliminated. Variable stoichiometry formulations are more important to accurately simulating nutrient recycling than to computing algal growth, so this scheme may be a reasonable compromise between the variable stoichiometry formulations discussed above and conventional fixed stoichiometry formulations.

6.5 RESPIRATION AND EXCRETION

Respiration and excretion are generally combined and modeled as a single term which includes all metabolic losses and excretory processes. These losses represent the difference between gross growth and net growth. Since net growth (rather than gross growth) is typically reported in the literature, some models lump respiration, excretion, and gross growth into a single net growth term, rather than simulating each process separately. However, it is generally more appropriate to compute growth and respiration separately since growth rates are sensitive to nutrient supplies while respiration rates depend primarily on temperature. Also, respiration and excretion are important components of nutrient recycling, so these processes are usually computed separately for use in the nutrient dynamic equations.

Most models express respiration (plus excretion) as either a constant loss term or as a function of temperature. The general expression is:

$$r = r(T_{\text{ref}}) f_r(T) \quad (6-68)$$

where r = rate of respiration plus excretion, 1/time
 $r(T_{\text{ref}})$ = respiration rate at a particular reference temperature
 T_{ref} , 1/time
 $f_r(T)$ = temperature function for respiration

The temperature functions for respiration use the same formulations discussed above for growth (Equations (6-5) through (6-25)). Most models use the same temperature function and coefficients for both processes. The major approaches are 1) linear increases in respiration with temperature, 2) exponential increases in respiration with temperature, and 3) temperature optimum curves in which respiration increases with temperature up to the optimum temperature and then decreases with higher temperatures. The most commonly used exponential formulation is the Arrhenius relationship with a reference temperature of 20°C (Equation (6-15a)). Some models, for example CE-QUAL-R1 (WES, 1982), use the left hand side of a temperature optimum curve or a logistic equation (Equation (6-22a)) to define temperature effects on respiration. This approach assumes respiration increases exponentially at low temperatures, but eventually levels off to some maximum value at higher temperatures.

A few models use formulations which relate the respiration rate to the physiological condition of the algal cells. For example, Scavia (1980) represents respiration as the sum of two components, 1) a low maintenance rate representing periods of minimal growth, and 2) a rate which is directly proportional to the photosynthesis rate (as defined by the growth limitation factor):

$$r(T_{\text{ref}}) = r_{\text{min}}(T_{\text{ref}}) + k_r(T_{\text{ref}}) f(L,P,N,C,Si) \quad (6-69)$$

where $r_{\text{min}}(T_{\text{ref}})$ = base respiration rate under conditions of minimal growth (poor physiological condition) at reference temperature T_{ref} , 1/time

$k_r(T_{\text{ref}})$ = maximum incremental increase in respiration under conditions of maximum growth (optimum physiological condition) at reference temperature T_{ref} , 1/time

Both rates are multiplied by a temperature adjustment function.

The MS.CLEANER model uses a similar formulation which expresses respiration as the sum of endogenous respiration and photorespiration

(Grodén, 1977; Park et al., 1980). The endogenous respiration is defined as:

$$r_e = .0175 e^{.069T} \quad (6-70)$$

where r_e = endogenous respiration rate, 1/time
 T = temperature, °C

Photorespiration is defined as a constant fraction of the temperature adjusted maximum photosynthesis rate in early versions of MS.CLEANER (Grodén, 1977):

$$r_p = K_{p1} \mu_{\max}(T_{\text{ref}}) f(T) \quad (6-71)$$

where r_p = photorespiration rate, 1/time
 K_{p1} = fraction of maximum photosynthesis rate which is oxidized by photorespiration (typically 5 to 15%)

and as a fraction of the actual photosynthesis rate (including temperature, light, and nutrient limitation effects) in later versions (Park et al., 1980):

$$\begin{aligned} r_p &= K_{p2} \mu \\ &= K_{p2} \mu_{\max}(T_{\text{ref}}) f(T) f(L,P,N,C,Si) \end{aligned} \quad (6-72)$$

where K_{p2} = fraction of actual photosynthesis rate which is oxidized by photorespiration

MS.CLEANER also considers excretion as a separate loss term, in contrast to most models which lump respiration and excretion together. Excretion is formulated similar to photorespiration. However, since the excretion of photosynthate and photorespiratory compounds relative to carbon assimilation (photosynthesis) is highest at both low light levels and inhibitory high light levels, the excretion rate is expressed as (Desormeau, 1978; Collins, 1980):

$$e_x = K_e (1 - f(L)) \mu \quad (6-73)$$

where e_x = excretion rate, 1/time

K_e = fraction of photosynthesis excreted

$f(L)$ = light limitation factor

μ = growth (photosynthesis) rate, including effects of temperature, light, and nutrient limitation, 1/time

Lehman et al. (1975), Jorgensen (1976), and Jorgensen et al. (1978, 1981) use variable stoichiometry formulations which relate the respiration rate to the internal carbon levels of the cells. The ratio of the internal carbon level to the maximum internal carbon level is used to define the physiological state of the cells. The respiration rate increases with the internal carbon level according to the equation:

$$r(T_{ref}) = r_{max}(T_{ref}) \left(\frac{C_{int}}{C_{max}} \right)^{2/3} \quad (6-74)$$

where $r_{max}(T_{ref})$ = maximum respiration rate at reference temperature
 T_{ref} , 1/time

C_{int} = internal carbon level, mass carbon/biomass algae

C_{max} = maximum internal carbon level, mass carbon/biomass algae

Algal respiration rates are tabulated in Table 6-18.

6.6 SETTLING

Phytoplankton settling rates depend on the density, size, shape, and physiological state of the phytoplankton cells, the viscosity and density of the water, and the turbulence and velocities of the flow field. The settling velocities for spherical particles in still water can be computed from Stoke's law. Stoke's law can be modified to account for non-spherical phytoplankton cells by using an "equivalent radius" and "shape factor" in the formulation (Scavia, 1980):

TABLE 6-18. ALGAL RESPIRATION RATES

Algal Type	Respiration Rate (l/day)	Reference Temperature (°C)	References
Total Phytoplankton	0.05 - 0.15	20°C	Di Toro <u>et al.</u> (1971, 1977) O'Connor <u>et al.</u> (1975, 1981) Thomann <u>et al.</u> (1974, 1975, 1979) Di Toro & Matystik (1980) Di Toro & Connolly (1980) Thomann & Fitzpatrick (1982) Salisbury <u>et al.</u> (1983)
	0.05 - 0.10	20°C	Chen & Orlob (1975) Chen & Wells (1975, 1976) Tetra Tech (1976)
	0.08	20°C	Canale <u>et al.</u> (1976)
	0.10	20°C	Lombardo (1972)
	0.088 - 0.6	T _{opt}	Jorgensen (1976) Jorgensen <u>et al.</u> (1978)
	0.051	20°C	Brandes (1976)
	0.05	20°C	Grenney & Kraszewski (1981)
	0.005 - 0.12*	20°C	Baca & Arnett (1976)
	0.05 - 0.2*	20°C	Smith (1978)
	0.05 - 0.5*	20°C	Roesner <u>et al.</u> (1980) Duke & Masch (1973)
	0.02 - 0.8*	20°C	Grenney & Kraszewski (1981)
	0.05 - 0.10**	20°C	Collins & Wlosinski (1983)
	0.05 - 0.20**	20°C	Jorgensen (1979)
Diatoms	0.04 - 0.08	20°C	Thomann <u>et al.</u> (1979) Di Toro & Connolly (1980) Salisbury <u>et al.</u> (1983) Di Toro <u>et al.</u> (1971)
	0.07 - 0.08	20°C	Porcella <u>et al.</u> (1983) Tetra Tech (1980)
	0.03 - 0.05	20°C	Bierman (1976) Bierman <u>et al.</u> (1980)
	0.05 - 0.25	T _{opt}	Scavia <u>et al.</u> (1976) Scavia (1980) Bowie <u>et al.</u> (1980)
	0.05 - 0.59**	20°C	Collins & Wlosinski (1983)
(continued)			

TABLE 6-18. (continued)

Algal Type	Respiration Rate (l/day)	Reference Temperature (°C)	References
Green Algae	0.05 - 0.07	20°C	Tetra Tech (1980) Porcella <i>et al.</i> (1983)
	0.05 - 0.25	T _{opt}	Scavia <i>et al.</i> (1976) Scavia (1980) Bowie <i>et al.</i> (1980)
	0.03 - 0.05	20°C	Bierman (1976) Bierman <i>et al.</i> (1980)
	0.01 - 0.46**	20°C	Collins & Wlosinski (1983)
Blue-green Algae	0.05 - 0.065	20°C	Tetra Tech (1980) Porcella <i>et al.</i> (1983)
	0.05 - 0.25	T _{opt}	Scavia <i>et al.</i> (1976) Scavia (1980) Bowie <i>et al.</i> (1980)
	0.03 - 0.05	20°C	Bierman (1976) Bierman <i>et al.</i> (1980)
	0.10 - 0.92**	20°C	Collins & Wlosinski (1983)
Dinoflagellates	0.047	20°C	O'Connor <i>et al.</i> (1981)
Flagellates	0.05	20°C	Bierman <i>et al.</i> (1980)
	0.05 - 0.06	20°C	Tetra Tech (1980) Porcella <i>et al.</i> (1983)
Chrysophytes	0.15 - 0.32**	20°C	Collins & Wlosinski (1983)
Benthic Algae	0.02 - 0.1	20°C	Tetra Tech (1980) Bowie <i>et al.</i> (1980) Porcella <i>et al.</i> (1983)
	0.44	T _{opt}	Auer and Canale (1982)
	0.1	20°C	Grenney & Kraszewski (1981)
	0.02 - 0.8*	20°C	Grenney & Kraszewski (1981)
	0.05 - 0.2*	20°C	Smith (1978)

*Model documentation values.

**Literature values.

$$V_s = \frac{2}{9} \frac{g R^2 (\rho_p - \rho_w)}{\nu F_s} \quad (6-75)$$

where V_s = settling velocity, length/time
 g = acceleration of gravity, length/time²
 R = equivalent radius (based on a sphere of equivalent volume),
length
 ρ_p = density of the cell, mass/length³
 ρ_w = water density, mass/length³
 ν = kinematic viscosity
 F_s = shape factor

The shape factor has a value ≥ 1.0 and accounts for all factors which reduce the settling velocities below that of an equivalent spherical particle, for example increased drag due to diatom spicules, flat or elongated cells, clusters or colonies of cells, etc. In a model of Lake Ontario, Scavia (1980) used a shape correction factor of 1.3 for small diatoms, 2.0 for large diatoms, and 1.0 for all other algal groups.

In practice, very few models use Stoke's law as a model formulation (Scavia et al., 1976; Scavia, 1980; Park et al., 1980). Most models lump many species into a few algal groups, so representative values of the cell radius, shape factor, and cell density are difficult to define, making this level of detail unnecessary. Since the shape factor is really a calibration parameter, it is more direct to simply use the settling velocity as a calibration parameter. Also, Stoke's law does not account for turbulence and flow velocities which tend to keep algae in suspension or resuspend settled algae. Additional factors which further complicate settling include the production of gas vacuoles or gelatinous sheaths which make some species buoyant, and the fact that settling velocities may vary with the nutritional state or physiological condition of the cells.

Settling rates are also partly dependent on the structure of the model. For example, one-dimensional layered lake models typically use settling velocities which are an order of magnitude lower than measured values or

values used in two-or three-dimensional models which simulate hydrodynamic processes (Scavia and Bennett, 1980). This is probably because one-dimensional models do not adequately represent vertical transport process such as upwelling or entrainment of phytoplankton in large-scale circulations which effectively reduce the net settling rates (Scavia and Bennett, 1980).

Because of the above factors, most models specify phytoplankton settling velocities directly as model coefficients. The settling rate in Equations (6-1) or (6-2) is generally expressed as:

$$s = \frac{V_s}{d} \quad (6-76)$$

where s = settling rate, 1/time

V_s = settling velocity, length/time

d = water depth, length

In layered models, algae settling in from the above layer, as well as algae settling out of the layer, must be included in the formulation. This also requires consideration of the bottom topography, since a fraction of the algae will settle onto the bottom area associated with each layer.

Equation (6-76) is refined in some models by including a temperature function which accounts for changes in settling velocities due to temperature effects on the density and viscosity of water. The settling rate is then expressed as:

$$s = \frac{V_s(T_{ref})}{d} f_s(T) \quad (6-77)$$

where $V_s(T_{ref})$ = settling velocity at reference temperature T_{ref} ,
length/time

$f_s(T)$ = temperature adjustment function for the settling
velocity

Typical examples of temperature adjustment functions include (Tetra Tech, 1980):

$$f_s(T) = \frac{157.5}{0.069T^2 - 5.3T + 177.6} \quad (6-78)$$

where T = temperature in $^{\circ}\text{C}$.

or (Scavia and Park, 1976):

$$f_s(T) = 1 + a_s T \quad (6-79)$$

where a_s = slope of settling velocity vs. temperature curve

Scavia et al. (1976) have also expanded the settling rate formulation to account for variations in settling velocities due to the physiological condition of the phytoplankton cells. The basic assumption is that the cells are healthiest and the settling rates smallest when neither light nor nutrients are limiting growth. The settling rates are therefore expressed as a function of the growth limitation factor $f(L,P,N,C,Si)$. Potential formulations include (Scavia et al., 1976; Scavia, 1980):

$$s = \frac{V_{s\max}(T_{\text{ref}})}{d} f_s(T) \left(\frac{K_{\text{set}_1}}{f(L,P,N,C,Si) + K_{\text{set}_1}} \right) \quad (6-80)$$

or

$$s = \frac{V_{s\max}(T_{\text{ref}})}{d} f_s(T) \left[1 - K_{\text{set}_2} f(L,P,N,C,Si) \right] \quad (6-81)$$

where $V_{s\max}(T_{\text{ref}})$ = maximum settling velocity at reference temperature
 T_{ref} under poor physiological condition,
length/time

$K_{\text{set}_1}, K_{\text{set}_2}$ = constants of the settling formulations

A few models require specification of the settling rate s rather than the settling velocity V_s as a model calibration coefficient. When used in

this way, the settling rate may take on a wide range of values since it depends as much on the water depth as the settling velocities of the algae.

Phytoplankton settling velocities are presented in Table 6-19. Additional data are available in a review by Smayda (1970).

6.7 NONPREDATORY MORTALITY

Nonpredatory mortality accounts for all algal losses which are not explicitly accounted for by the grazing term or other loss processes in the model (for example, settling and respiration if they are not computed explicitly). Nonpredatory mortality includes processes such as senescence, bacterial decomposition of cells (parasitism), and stress-induced mortality due to severe nutrient deficiencies, extreme environmental conditions, or toxic substances. The nonpredatory mortality rate in Equations (6-1), (6-2), or (6-3) is generally specified as a constant model coefficient. This is in contrast to the predatory mortality or grazing rate which is computed dynamically to reflect changes in the predator densities.

In some models, a temperature adjustment function is used with nonpredatory mortality which results in:

$$m = m(T_{\text{ref}}) f_m(T) \quad (6-82)$$

where m = nonpredatory mortality rate, 1/time

$m(T_{\text{ref}})$ = nonpredatory mortality rate at reference temperature

T_{ref} , 1/time

$f_m(T)$ = temperature function for mortality

The temperature functions for mortality generally use the same formulations used for growth and respiration (Equations (6-5) through (6-25)). However, if a temperature optimum curve is used for growth, the temperature function for mortality will often use only the left hand portion of the curve to produce a temperature response curve in which mortality increases with temperature until some maximum mortality rate is reached.

TABLE 6-19. PHYTOPLANKTON SETTLING VELOCITIES

Algal Type	Settling Velocity (m/day)	References
Total Phytoplankton	0.05 - 0.5	Chen & Orlob (1975) Tetra Tech (1976) Chen (1970) Chen & Wells (1975, 1976)
	0.05 - 0.2	O'Connor <u>et al.</u> (1975, 1981) Thomann <u>et al.</u> (1974, 1975, 1979) Di Toro & Matystik (1980) Di Toro & Connolly (1980) Thomann & Fitzpatrick (1982)
	0.02 - 0.05	Canale <u>et al.</u> (1976)
	0.4	Lombardo (1972)
	0.03 - 0.05	Scavia (1980)
	0.05	Bierman <u>et al.</u> (1980)
	0.2 - 0.25	Youngberg (1977)
	0.04 - 0.6	Jorgensen (1976) Jorgensen <u>et al.</u> (1978, 1981)
	0.01 - 4.0*	Baca & Arnett (1976)
	0. - 2.0*	Chen & Orlob (1975) Smith (1978)
	0.15 - 2.0*	Duke & Masch (1973) Roesner <u>et al.</u> (1977)
	0. - 0.2*	Brandes (1976)
	0. - 30.**	Jorgensen (1979)
Diatoms	0.05 - 0.4	Bierman (1976) Bierman <u>et al.</u> (1980)
	0.1 - 0.2	Thomann <u>et al.</u> (1979) Di Toro & Connolly (1980)
	0.1 - 0.25	Tetra Tech (1980) Porcella <u>et al.</u> (1983)
	0.03 - 0.05	Canale <u>et al.</u> (1976)
	0.3 - 0.5	Smayda & Boleyn (1965)
	2.5	Lehman <u>et al.</u> (1975)
	0.02 - 14.7**	Collins & Wlosinski (1983)
	0.08 - 17.1**	Jorgensen (1979)
(continued)		

TABLE 6-19. (continued)

Algal Type	Settling Velocity (m/day)	References
Green Algae	0.05 - 0.19	Jorgensen <u>et al.</u> (1978)
	0.05 - 0.4	Bierman (1976) Bierman <u>et al.</u> (1980)
	0.02	Canale <u>et al.</u> (1976)
	0.8	Lehman <u>et al.</u> (1975)
	0.1 - 0.25	Tetra Tech (1980) Porcella <u>et al.</u> (1983)
	0.3	DePinto <u>et al.</u> (1976)
	0.08 - 0.18**	Collins & Wlosinski (1983)
	0.27 - 0.89**	Jorgensen (1979)
Blue-green Algae	0.05 - 0.15	Bierman (1976) Bierman <u>et al.</u> (1980)
	0.	Canale <u>et al.</u> (1976)
	0.2	Lehman <u>et al.</u> (1975)
	0.1	DePinto <u>et al.</u> (1976)
	0.08 - 0.2	Tetra Tech (1980) Porcella <u>et al.</u> (1983)
	0.10 - 0.11**	Collins & Wlosinski (1983)
Flagellates	0.5	Lehman <u>et al.</u> (1975)
	0.05	Bierman <u>et al.</u> (1980)
	0.09 - 0.2	Tetra Tech (1980) Porcella <u>et al.</u> (1983)
	0.07 - 0.39**	Collins & Wlosinski (1983)
Dinoflagellates	8.0	O'Connor <u>et al.</u> (1981)
	2.8 - 6.0**	Collins & Wlosinski (1983)
Chrysophytes	0.5	Lehman <u>et al.</u> (1975)
Coccolithophores	0.25 - 13.6	Collins & Wlosinski (1983)
	0.3 - 1.5**	Jorgensen (1979)

*Model documentation values.

**Literature values.

A few models use more sophisticated formulations for nonpredatory mortality which try to relate the mortality rate to the physiological condition of the algal cells or to the size of the decomposer population (De Pinto, 1979). For example, Scavia et al. (1976) use the value of the growth limitation factor $f(L,P,N,C,Si)$ as a measure of cell health and express the mortality rate as:

$$m(T_{ref}) = m_{max}(T_{ref}) [1 - f(L,P,N,C,Si)] \quad (6-83)$$

where $m_{max}(T_{ref})$ = maximum nonpredatory mortality under poor physiological conditions at reference temperature T_{ref} , 1/time

This assumes minimal mortality and algal decomposition when growth conditions are optimal, and maximum mortality when conditions are severely limiting.

Lehman et al. (1975) use a similar approach, but also include the duration of growth limiting conditions in the formulation. They define the mortality rate as:

$$m(T_{ref}) = m_{max}(T_{ref}) \left(1 - e^{-K_{so}T_{so}}\right) \quad (6-84)$$

where T_{so} = number of days of suboptimal conditions (defined as $\mu/\mu_{max} < 0.05$), time

K_{so} = coefficient defined as $\ln 2$ divided by the number of days at suboptimal conditions until m increases to $\frac{1}{2} m_{max}$

MS.CLEANER expresses nonpredatory mortality as a function of both the internal nutrient concentrations and temperature such that the mortality rate increases exponentially under conditions of either nutrient starvation or critically high temperatures. The equation is (Desormeau, 1978; Park et al., 1980):

$$m = K_m e^{K_n(N_{crit} - f(P,N,C,Si))} e^{(T - T_{crit})} \quad (6-85)$$

where K_m = nonpredatory mortality rate coefficient, 1/time
 K_n = exponent for nutrient starvation
 $f(P,N,C,Si)$ = variable stoichiometry nutrient limitation factor
for algal growth
 N_{crit} = critical value of $f(P,N,C,Si)$ for starvation
mortality
 T_{crit} = critical temperature for nonpredatory mortality

This assumes that when the internal nutrient levels drop below the subsistence quota, increased senescence, bacterial colonization, and cell lysis occur.

Bierman et al. (1980) use a nonpredatory mortality function which indirectly includes the size of the decomposer bacteria population in the formulation. Although the bacteria are not modeled explicitly, they are assumed to increase in proportion to the total algal concentration (the sum of all algal groups in the model). Therefore, increases in the bacteria associated with the bloom of one algal group will result in higher mortality rates for all other groups since a higher decomposer population is established. The equation is:

$$m(T_{ref}) = K_m(T_{ref}) \sum_{i=1}^n A_i \quad (6-86)$$

where $K_m(T_{ref})$ = nonpredatory mortality rate coefficient at reference
temperature T_{ref} , 1/time-algae

A_i = concentration of algal group i , mass/volume
 n = total number of algal groups

Nyholm (1978) uses a Michaelis-Menten type saturation function of the algal concentrations in his formulation for algal mortality:

$$m(T_{ref}) = m_{max}(T_{ref}) \left(\frac{A}{K_{m1} + A} \right) \quad (6-87)$$

where $m_{\max}(T_{\text{ref}})$ = maximum nonpredatory mortality rate at reference temperature T_{ref} , 1/time
 A = algal concentration, mass/volume
 K_{m1} = half-saturation constant for algal nonpredatory mortality, mass/volume

At high algal concentrations, this is equivalent to the basic first order formulation (Equation (6-82)), while at very low algal levels, the mortality rate is essentially a second order relationship analogous to Equation (6-86). However, even though the mortality rate is second order at low algal densities, the Michaelis-Menten term reduces the net rate at low densities below the maximum first-order rate at high algal densities.

The Michaelis-Menten formulation is also used by Di Toro and Matystik (1980), Di Toro and Connolly (1980), and Thomann and Fitzpatrick (1982) in their formulation for the decomposition of organic matter (dead algal cells), although a basic first-order formulation is used for algal nonpredatory mortality. These models use the Michaelis-Menten formulation to account for the effects of the bacterial population on decomposition rates, assuming that decomposers (and the resulting decomposition rates) increase in proportion to the algal densities at low concentrations, but that other factors limit decomposition rates at high algal densities (Di Toro and Matystik, 1980; Di Toro and Connolly, 1980). These mechanisms could also be assumed for nonpredatory mortality.

Rodgers and Salisbury (1981) use a modified Michaelis-Menten formulation for nonpredatory mortality which includes the effects of both bacterial activity and the physiological condition of the algal cells on algal decomposition:

$$m(T_{\text{ref}}) = m_{\max}(T_{\text{ref}}) \left(\frac{A/\mu}{K_{m2} + A/\mu} \right) \quad (6-88)$$

where μ = algal growth rate, 1/time
 K_{m2} = half-saturation constant for algal nonpredatory mortality, mass-time/volume

The mortality rate is directly proportional to the algal biomass (an indicator of bacterial activity) and inversely proportional to the algal growth rate (an indicator of the physiological condition of the cells), both through a saturation type relationship which limits the maximum rate.

Some models include formulations to account for stress-induced mortality due to factors such as extreme temperatures or toxic substances. Stress related mortality is typically modeled by expanding the nonpredatory mortality term to include additional terms for these effects, for example:

$$m = m(T_{ref}) f_m(T) + m_T(T_{ref}) f_T(T) + m_x f_x(X) \quad (6-89)$$

where $m_T(T_{ref})$ = thermal mortality rate at reference temperature
 T_{ref} , 1/time

$f_T(T)$ = thermal mortality response curve

m_x = toxic mortality rate, 1/time

$f_x(X)$ = dose-response curve for toxic mortality

X = concentration of toxicant, mass/volume

Toxic effects can also be included in the growth and respiration formulations.

Algal nonpredatory mortality rates are presented in Table 6-20.

6.8 GRAZING

Algal grazing losses can be modeled in several ways, depending on 1) whether predator populations are simulated in the model, and 2) whether alternate food items are available for the predators.

When predators are not explicitly modeled, predator-prey dynamics cannot be simulated, so grazing effects are typically handled by either assuming a constant grazing loss which is specified by the user as a model input parameter:

TABLE 6-20. ALGAL NONPREDATORY MORTALITY RATES

Algal Type	Nonpredatory Mortality Rate (1/day)	References
Total Phytoplankton	0.02	Thomann & Fitzpatrick (1982)
	0.003 - 0.17	Baca & Arnett (1976)
	0.03	Scavia <u>et al.</u> (1976)
	0.005 - 0.10	Salas & Thomann (1978)
	0.01 - 0.1	Jørgensen (1976) Jørgensen <u>et al.</u> (1978)
Diatoms	0.03	Scavia <u>et al.</u> (1976)
Benthic Algae	0. - 0.8	Tetra Tech (1980) Bowie <u>et al.</u> (1980) Porcella <u>et al.</u> (1983)

$$G = \text{constant} \quad (6-90)$$

where G = loss rate due to grazing, mass algae/time

or by assuming a loss rate which is directly proportional to the algal densities (e.g., RECEIV-II (Raytheon, 1974)):

$$G = e_z A \quad (6-91)$$

or
$$G = e_z(T_{\text{ref}}) f_g(T) A \quad (6-92)$$

where e_z = grazing rate coefficient, 1/time

A = algal biomass or density, mass or mass/volume

$e_z(T_{\text{ref}})$ = grazing rate coefficient at reference temperature
 T_{ref} , 1/time

$f_g(T)$ = temperature function for grazing

The second formulation is equivalent to that often used for non-predatory mortality (Equation (6-82)), so both nonpredatory mortality and grazing losses are typically combined into a single total mortality term when predator populations are not directly simulated:

$$\begin{aligned} m_{\text{tot}} &= \left(m(T_{\text{ref}}) + e_z(T_{\text{ref}}) \right) f_m(T) \\ &= m_{\text{tot}}(T_{\text{ref}}) f_m(T) \end{aligned} \quad (6-93)$$

where m_{tot} = total mortality rate, 1/time
 $m_{\text{tot}}(T_{\text{ref}})$ = total mortality rate at reference temperature T_{ref} ,
 1/time
 $f_m(T)$ = temperature function for mortality

The temperature functions used for grazing are the same as those discussed previously for algal growth, respiration, and mortality (Equations (6-5) to (6-25)).

Many general water quality models include a single zooplankton group to provide a more realistic grazing formulation for algae (Baca et al., 1973; Johanson et al., 1980; Najarian and Harleman, 1975). The zooplankton are often added only to obtain better simulations of algal dynamics, rather than to evaluate the zooplankton dynamics of the system. The coupled algae and zooplankton equations provide the major features of predator-prey interactions since the algal grazing rate is defined as a function of the zooplankton density which in turn varies dynamically with the food supply (algal concentration). The algal grazing rate in these models is typically expressed either in terms of a zooplankton filtration rate:

$$G = C_f A Z \quad (6-94)$$

$$\text{or} \quad G = C_f(T_{\text{ref}}) f_g(T) A Z \quad (6-95)$$

where C_f = zooplankton filtration rate, water volume/mass
 zooplankton-time

Z = zooplankton biomass or concentration, mass or mass/volume

$C_f(T_{ref})$ = filtration rate at reference temperature T_{ref} , water volume/mass zooplankton-time

or in terms of a zooplankton ingestion rate:

$$G = C_g Z \quad (6-96)$$

or
$$G = C_g(T_{ref}) f_g(T) Z \quad (6-97)$$

where C_g = zooplankton ingestion rate, mass algae/mass zooplankton-time

$C_g(T_{ref})$ = ingestion rate at reference temperature T_{ref} , mass algae/mass zooplankton-time

Ingestion rates are often back-calculated from computed zooplankton growth rates based on the equation (Chen and Orlob, 1975; Smith, 1978; Tetra Tech, 1979; WES, 1982):

$$C_g = \frac{g_z}{E} \quad (6-98)$$

where g_z = zooplankton growth rate, 1/time

E = zooplankton assimilation efficiency

In this approach, zooplankton growth rates are first computed as a function of food supply and temperature, and then the amount of algae which would have to be consumed to produce the growth is computed from Equation (6-98). The alternative approach is to specify or compute the ingestion rates directly, and then calculate the zooplankton growth rates based on the amount of food consumed and the assimilation efficiencies. Specific formulations for zooplankton filtration rates, ingestion rates, growth rates, and assimilation efficiencies are discussed in detail in Chapter 7.

Models which simulate only a single algal and zooplankton group tend to oversimplify predator-prey dynamics since a single constituent represents all primary producers and another single constituent represents all consumers. This ignores the complexities of the food web, as well as differences in foraging strategies, grazing rates, and food preferences between different types of predator organisms. This approach may be adequate in short term simulations where one group of phytoplankton and zooplankton are dominant. However, in long term simulations, more than one group of algae and zooplankton should be used to adequately simulate predator-prey interactions and population dynamics.

Algal grazing rates in multi-group models are functions of alternative food sources and food preferences, as well as predator densities, algal densities, and temperature. The basic grazing formulations are essentially the same as those mentioned above for a single zooplankton group, except that 1) grazing losses must be considered for each potential predator which grazes the algae, and 2) total grazing rates calculated for a given predator must be partitioned among the various food items which it consumes. Some models also consider differences in the ingestion or assimilation efficiencies between different food items (Scavia et al., 1976; Park et al., 1980), and differences in the feeding behavior of different zooplankton groups (e.g., non-selective filterers, selective filterers, carnivorous raptors, omnivores, etc.) (Canale et al., 1975, 1976; Park et al., 1980).

Grazing losses for non-selective feeders can be partitioned between different algal groups by distributing them in proportion to the algal concentrations:

$$G_{ij} = C_j \frac{A_i}{\sum_{k=1}^n F_k} Z_j \quad (6-99)$$

where G_{ij} = loss rate of algal group i due to grazing by zooplankton group j , mass algae/time

C_j = total ingestion rate of zooplankton group j on all food items, mass food/mass zooplankton-time

A_i = biomass or concentration of algal group i , mass or mass/volume

F_k = biomass or concentration of potential food item k consumed by zooplankton group j , mass or mass/volume

n = number of potential food items

Z_j = biomass or concentration of zooplankton group j , mass or mass/volume

When grazing is expressed in terms of a filtration rate this partitioning is done automatically since the grazing losses are simply the algal concentrations times the volumetric filtration rates.

The above expression can be modified to account for selective feeding behavior by using food preference factors. These are weighting factors which reflect the probability that a given food will be consumed relative to the others when all foods are present in equal concentrations. The preference factors account for feeding differences due to factors like food particle size and shape, desirability and quality of food, and zooplankton feeding behavior. The grazing losses for each algal group subject to selective feeding can be expressed as:

$$G_{ij} = C_j \frac{P_{ij} A_i}{\sum_{k=1}^n P_{kj} F_k} Z_j \quad (6-100)$$

where P_{ij} = preference factor for zooplankton j grazing on algal group i

P_{kj} = preference factor for zooplankton j grazing on food item k

The total ingestion rates C_j for each predator are the same as discussed above for a single zooplankton group (Equations (6-94) through (6-98)).

When several predators are modeled, the total grazing loss for a given algal group is the sum of the grazing losses from each predator:

$$G_i = \sum_{j=1}^{n_p} G_{ij} \quad (6-101)$$

where G_i = loss rate for algal group i due to grazing by all predators,
mass algae/time

n_p = total number of predators grazing on algal group i

Any of the previous formulations can be used to define the incremental grazing rates G_{ij} associated with each predator.

Zooplankton grazing rates are tabulated in Chapter 7, along with more detailed descriptions of the grazing formulations for zooplankton.

6.9 SUMMARY

Phytoplankton and attached algae are generally modeled as a biomass pool using the same mass balance approach used for nutrients and other constituents. The simpler models lump all algae into a single group, while more complex models distinguish between different functional groups such as green algae, diatoms, and blue-green algae. Single-group models are commonly used in rivers, while multi-group models are more common in lakes where long-term simulations of the seasonal succession of different types of phytoplankton are important.

Algal dynamics depend on growth, respiration, excretion, settling, nonpredatory mortality, and predation. Although some of these processes can be measured in the field or laboratory, most of the coefficients defining the process rates are usually determined by model calibration. This is necessary since the rates will vary with environmental conditions such as temperature, light, nutrient concentrations, and predator densities as well as with the species composition of the algae, all of which change continually with time. Literature values from laboratory experiments are useful for establishing reasonable ranges for the coefficients. However,

specific experimental results are difficult to apply directly since experiments typically use a single species rather than the species assemblages represented in models, and since experimental conditions may not represent conditions in the field. Model constructs must be relied upon to describe the effects of changing environmental and ecological conditions on the process rates.

Most processes in algal models are assumed to be temperature dependent. Three major approaches have been used to describe these effects: linear temperature response curves, exponential curves, and temperature optimum curves. The exponential Arrhenius relationship is commonly used when only one algal group is simulated, while temperature optimum curves are more common in multi-group models.

The most important and complex formulations in algal models are the growth formulations. Growth is a function of temperature, light, and nutrients. Light limitation is typically defined by either a saturation type relationship or a photoinhibition relationship in which growth decreases at light intensities above the optimum. Most models use Michaelis-Menten kinetics to describe nutrient limitation effects and assume the nutrient composition of the algal cells remains constant. More sophisticated models allow the internal stoichiometry of the algae to vary with changes in the external nutrient concentrations. These models simulate nutrient uptake and algal growth as two separate steps. Nutrient uptake is first computed as a function of both the internal nutrient levels in the cells and the external concentrations in the water. Algal growth is then computed based on the internal nutrient concentrations in the cells. Various formulations have been used to describe uptake and growth kinetics in variable stoichiometry models. These formulations are more complex and involve more model coefficients than fixed stoichiometry models.

Most models use simple temperature-dependent first-order relationships to describe respiration, settling, and nonpredatory mortality. A few models include the effects of the physiological condition of the algae on these processes by making them a function of the growth rate, growth limitation factor, or internal nutrient level (in variable stoichiometry models). Some

models also include the effects of the decomposer bacteria population on nonpredatory mortality. These latter effects are modeled indirectly by assuming the decomposers increase in proportion to the algal densities and using algal concentrations as an indicator of the bacterial population, rather than by simulating the decomposers directly. Both second-order mortality formulations and Michaelis-Menten type saturation relationships have been used to describe these effects.

Algal grazing is usually modeled as a first-order loss when zooplankton are not simulated. When zooplankton are modeled, algal grazing is a function of the algal densities, zooplankton densities, and the zooplankton filtration rates or consumption rates. In multi-group models which include several algal and zooplankton groups, selective feeding behavior can be simulated by including food preference factors in the grazing formulations.

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